ECOLOGICAL STUDIES OF TROPICAL SEMI-EVERGREEN RAIN FOREST AT SAKAERAT, NAKHON RATCHASIMA, NORTHEAST THAILAND, I. VEGETATION PATTERNS

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ABSTRACT

Quantitative data on species of trees and shrubs and environmental characteristics were obtained in 12 stands of tropical semi-evergreen rain forest at Sakaerat Environmental Research Station, Nakhon Ratchasima Province, NE Thailand. A polythetic agglomerative cluster analysis was used to classify sample stands into two dominance-types according to their dominant species: the *Hopea ferrea* type and the *Shorea henryana* type. The basal area and density of all stems (10 cm dbh) differed slightly between the two types (30m²/ha and 562 trees/ha, respectively, in the *Hopea ferrea* type and 27 m²/ha and 514 trees/ha in the *Shorea henryana* type). Half of the species of the two types were indentical. Indirect ordination also separated the sample stands into the same two groups as cluster analysis. Both groups were related to gradients of moisture and fertility (including Ca, P, organic matter). The *Hopea ferrea* type was characterized by low calcium and high moisture content while the *Shorea henryana* type was characterized by high calcium but low mois ture content.

Size-class analysis indicated a similar structure in the two dominance-types. Both were well described by a negative power curve and negative exponential distribution. Size-class distrigutions of individual species exhibited variable patterns.

Topographic and soil parameters were used for stepwise multiple regressions to develop predictive equations for the distribution of tree species. Species distributions were related to soil fertility and elevation while community distribution was related to moisture content and soil fertility.

INTRODUCTION

The tropical semi-evergreen rain forest (WHITMORE, 1984) is usually referred to as the dry evergreen forest by the ROYAL FOREST DEPARTMENT OF THAILAND (1962). Tree species in this forest are mainly evergreen. In the upper tree layer, trees achieve a height of 35 m and are moderately drought resistant, while some shed leaves during the dry season. In the undergrowth, tree seedlings, saplings and shrubs are abundant and mostly evergreen. Epiphytes and lianas are present.

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At Sakaerat Environmental Research Station, tropical semi-evergreen rain forest is the main forest type. It covers 36% (30 km²) of the total area (WACHARAKITTI, INTRACHANDRA & MUNGKORNDIN, 1980). Although there have been many studies in this forest type at Sakaerat, only one was concerned with forest structure (VISARATANA, 1983). The objectives of the present study are (1) to determine vegetation structure and composition, and (2) to assess environmental relationships in determining species distributions.

STUDY AREA

Sakaerat Environmental Research Station, encompassing a reserved area of 81 km², is located on the eastern edge of the Phuluang Reserved Forest in Pak Thongchai District, Nakhon Ratchasima Province, NE Thailand. The site lies on the west side of Highway No. 304, 60 km south of Nakhon Ratchasima City (latitude 14° 31' N, longitude 101° 55' E) (Fig. 1). Topographically, the forest area mainly comprises slopes of 4.5°-20° but there is also a small flat area.

The sedimentary rock in the study area is a sandstone formed in the Triassic to Cretaceous periods and is classified in the Khorat group (*Phra wihan* formation) (MOORMANN & ROJANASOONTHON, 1972). Upper soil texture is characterized as clay loam, sandy loam, and sandy clay loam. Lower soils are clayey. The parent material is sandstone, which always occurs in the soil profile. Soil thickness varies from 70 to 100 cm or more.

The climate at the site is monsoonal. Walter's climate diagram for the study area is shown in Fig.2. Average annual rainfall is 1,240 mm, with May through October receiving greater than 100 mm per, month. Mean temperature is 26.2°C with an average monthly minimum of 21.6°C in December and a maximum of 28.7°C in March.

METHODS

Field and Laboratory Procedures

Twelve stands (1 km² per stand exclusive of ecotones) that exhibited no signs of recent disturbance and were relatively homogeneous in species composition and distribution were chosen. In each stand, two 20×50 m sample plots in an east-west direction were placed parallel to each other and 10 m apart. Each sample plot was subdivided into ten 10×10 m subplots. Within each of these subplots, one 4×4 and one 1×1 m plot were placed at the lower right corner. Sample units were nested rectangular plots: 100 m^2 for stems $\geqslant 10 \text{ cm}$ dbh (trees) and stems 4.5 to 10 cm dbh (small trees), 16 m^2 for stems less than 4.5 cm dbh and more than 1.30 m tall (saplings and shrubs), and 1 m^2 for tree and shrub seedlings less than 1.30 m tall.

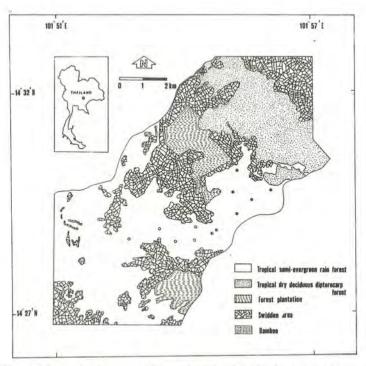


Figure 1. Map of Sakacrat Environmental Research station Showing location of *Hopea ferrea* (•)

Shorca henryana (()), and ecotone (()) sample plots.

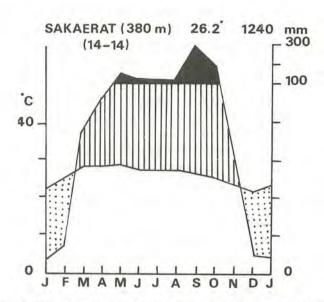


Figure 2. Climate diagram (1969-1982) of Sakaerat Environmental Research Station, Nakhon Rachasima.

The basal area of trees ≥ 4.5 cm dbh of each species was computed from the dbh measurement of those within the twenty 100-m^2 subplots in each stand. Stems < 4.5 cm dbh were counted only. For each stand, elevation, slope and aspect were determined.

One soil pit was dug at the centre of each sample plot, and soil samples were collected at depths of 0-5, 10-15, 20-25, 30-35, 45-50 and 70-75 cm. They were air-dried and passed through a 2-mm sieve. Composites of two collections at the same depth in each stand were mixed and analyzed for physical and chemical properties. Texture was determined by the hydrometer method (BOUYOUCOS, 1951). Soil pH was determined by a 1:1 soil-to-water suspension with a pH meter. Available P was extracted by Bray's II method. Exchangeable K and Na were determined by flame photometry and exchangeable Ca and Mg determined by an atomic absorption spectrophotometer. Cation exchange capacity was determined by using a neutral normal ammonium acetate extraction. Available moisture capacity was determined as the difference between water content of the soil at 1/3 and 15 bars. Bulk density was determined by the core method.

Data Analysis

As an initial step towards classification, 2-dimensional ordination (BRAY & CURTIS, 1957) of the 12 stands using species (\geqslant 10 cm dbh) importance values 300 (IV = relative density + relative basal area + relative frequency) was conducted to determine gradients of species composition and environmental influences. Indirect gradient analysis was determined by simple linear correlation of environmental factors against sample axis scores. The same data set used for ordination was also used to classify sample stands into groups by cluster analysis. A polythetic agglomerative cluster analysis was originally proposed by SOKAL & MICHENER (1958). It has been used to classify sample stands into groups based on the similarity of the stands. Individual stands are compared to one another, the stand-pair with the highest similarity value is fused into a group by averaging the quantitative values of each species in the two stands. That pair becomes a new group and the procedure is continued until all stands are fused into one hierarchical broad cluster. Size-class distributions were constructed using size-classes \geqslant 4.5 to < 10 cm dbh and successive 10-cm increments in dbh.

Species-environment relationships were determined by stepwise multiple regression. Importance values of the species were the dependent variables. Independent variables consisted of: bulk density, percent silt + clay, soil pH, percent organic matter, available phosphorus, exchangeable potassium, calcium, magnesium, and sodium, cation exchange capacity, and available moisture capacity of surface soil (0-15 cm depth), elevation and slope. Since the number of observations (n) was less than number of independent variables, after the regression equations were predicted, a number of

independent variables (n-2) of each species were selected and used to recalculate the new predictive regression equation of those species.

RESULTS

Forest Structure and Composition

The ordination of the tropical semi-evergreen rain forest at Sakaerat produced a readily interpretable distribution of sample stands. Two distinct groups were recognized (Fig.3). Comparison of the classification from the dendrogram (Fig.4) with the Bray-Curtis ordination (Fig.3) showed that the two approaches agreed in the arrangement of stands. The stand groupings in the ordination also appeared in the dendrogram. The groups could be designated by dominant tree species: the *Hopea ferrea* type and the *Shorea henryana* type.

Hopea ferrea type. This dominance-type comprised four vertical layers: trees, small trees, saplings and shrubs, and undergrowth. Usually, the tree layer comprised two strata. The upper stratum, usually 30-35 m high but sometimes reaching 40 m, was strongly dominated by Hopea ferrea Pierre. Other associated species were Shorea henryana Pierre, Irvingia malayana Oliv. ex A. Benn., Lagerstroemia duperreana Pierre, Eugenia cumini Druce, and Dialium cochinchinensis Pierre. The lower stratum was 16-22 m high and also dominated by Hopea ferrea. Other common species were Hydnocarpus ilicifolius King, Walsura trichostemon Miq., Memecylon ovatum J.E. Smith, Aglaia pirifera Hance, Hydnocarpus castaneus Hook.f. & Th., Phoebe sp. and Adenanthera pavonina Linn. The middle tree stratum was poorly developed.

The small tree layer was 7-14 m high, and provided a continuous canopy. Five species were dominant in this layer: Hydnocarpus ilicifolius, Memecylon ovatum, Hopea ferrea, Walsura trichostemon, Aglaia pirifera, along with Memecylon geddesianum Craib, Hydnocarpus castaneus, Linociera microstigma Gagnep and Randia wittii Craib.

The sapling and shrub layer was generally dense except in rock outcrop areas, with saplings of *Hopea ferrea* and other species of the tree layers. The scattered herbs included *Fimbristylis dipsacea* Clarke, *Rhaphidophora peepla* Schott, and *Zingiber* spp. *Apluda mutica* Linn. was the dominant grass occurring in the open areas and on the trail side. Lianas frequently occurred in this type; *Ancistrocladus tectorius* Merr. was the most important and commonly climbed to the top of the upper canopy. Other lianas were *Ventilago harmandiana* Pierre, *Strychnos kerrii* A.W. Hill, *Tournefortia intonsa* Kerr. *Gnetum* sp. and *Hymenopyramis* sp. Epiphytes were found on large limbs and tree trunks. Some mosses occurred on both the tree trunks and the ground. Species composition of the stands adjacent to the dry deciduous dipterocarp forest was different from the rest. The small tree layer and sapling and shrub layer were dense with *Acacia pennata* Willd. and *Acacia comosa* Gagnep. This indicates that those stands

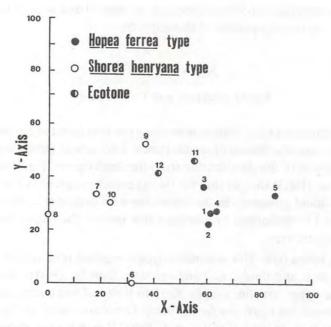


Figure 3. Distribution of sample stands relative to the first and second axes of ordination.

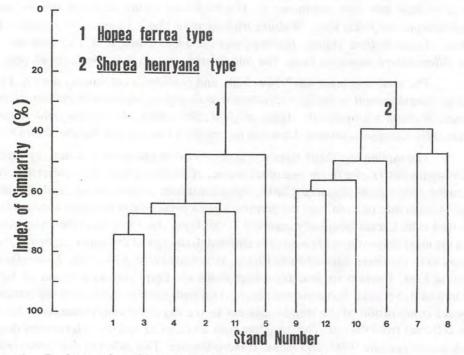


Figure 4. Dendrogram formed by agglomerative cluster analysis of 12 stands.

were drier than more typical stands. Generally, the *Hopea ferrea* type occupied flat areas, although some stands occurred on moderate slopes.

Shorea henryana type. Vertical structure was similar to that of the Hopea ferrea type but was richer and different in species composition, notably with the absence of Hopea ferrea. The tree layer was also composed of upper and lower strata. The upper stratum was 30-40 m high, dominated by Shorea henryana and including Quercus myrsinifolia Bl., Dipterocarpus turbinatus Gaertn.f., Irvingia malayana, Parkia sumatrana Miq. Dialium cochinchinensis, Eugenia cumini and Hopea helfeti Brand. The middle stratum was poorly developed. The lower stratum was dominated by the same species, with a height of 17-22 m. Other common species were the same as in the lower tree stratum of the Hopea ferrea type but without Hopea ferrea, and mixed with Cleidion spiciflorum Merr., Knema globularia Warb., Garcinia speciosa Wall., Tarenna collinsae Craib and Adenanthera pavonina Linn.

The small tree layer was 7-15 m high and formed a continuous crown cover. Its species composition was the same as the lower tree stratum including Schoutenia hypoleuca Pierre, Acacia pennata and Lepisanthes tetraphylla Radlk. The sapling and shrub layer was composed of saplings of the tree layer species. Seedlings in the undergrowth layer were not so dense as in the Hopea ferrea type. Herbs, grasses, and lianas were similar to the previous type. However, more species of lianas were observed, including Bauhinia scandens Linn. var. horsfieldii K. & S. Larsen, Toddalia asiatica Lamk. and Neuropeltis racemosa Wall. The palms Caryota urens Linn., Areca sp., Calamus viminalis Willd. and Calamus myrianthus Bece. were common, as were epiphytes.

Typically, the *Shorea henryana* type occupied mountainous areas of moderate to steep slope. Generally speaking, bamboo was not common in the tropical semi-evergreen rain forest. However, a bamboo, *Gigantochloa albociliata* Munro, occurred in one stand of the *Shorea henryana* type which had a large gap due to windthrow. The bamboo seeds were probably dispersed here from a bamboo forest not far from the stand.

An ecotone of about 300-500 m in width existed between the two dominance-types. Here, the vertical structure was similar to both types. *Hopea ferrea* became gradually less important as one moved from the *Hopea ferrea* type to the *Shorea henryana* type. Some rare species in the *Hopea ferrea* type, e.g. *Quercus myrsinifolia* and *Garcinia* sp., occurred frequently in the ecotone.

The composition of the two dominance-types and the ecotone is shown in Table 1. Total basal area and density of trees \geq 10 cm dbh were greater in the *Hopea ferrea* type (30 vs 27 m²/ha and 562 vs. 514 trees/ha). In contrast, total basal area and density of trees < 10 cm dbh were less in the *Hopea ferrea* type (2.2 vs. 2.8 m²/ha and 592 vs. 768 trees/ha). However, the difference was not statistically significant.

Half of the floristic composition of the two types was the same. Ninety-two tree and shrub species were present in the study stands; 59 of these occurred in the

Table 1. Species composition, density (trees/ha, 4.5 - < 10 cm and ≥ 10 dbh) and basal area (m²/ha, 4.5 - < 10 cm and ≥ 10 cm dbh) in the three groups identified for the tropical semi-evergreen rain forest in Fig. 3 and 4.

	Hopea ferrea type				Shorea henryana type				Ecotone			
	Densit	y	Basai	area	Density		Basal area		Density		Basal	area
Species	4.5 -<10	≥10	4.5 -<10	≱ 10	4.5 -<10	≱10	4.5 -<10	≽ 10	4.5-<	0 >10	4.5 -<1	0 ≥10
Hopea ferrea Pierre	69	185	0.27	16.12	-	-	-	-	65	122.5	0.23	7.86
Shorea henryana Pierre	2	7	0.006	1.39	5	36	0.02	6.81	2.5	27.5	0.006	4.61
Hydnocarpus ilicifolius King	77	75	0.30	1.53	27	35	0.10	0.91	62.5	92.5	0.24	2.08
Walsura trichostemon Miq.	72	30	0.27	0.54	87	34	0.29	0.57	75	35	0.28	0.62
Memecylon ovatum J.E. Smith	65	31	0.28	0.54	38	27	0.15	0.41	30	7.5	0.09	0.09
Aglaia pirifera Hance	59	19	0.19	9.75	17	29	0.06	1.03	47.5	82.5	0.14	2.89
Hydnocarpus castaneus Hook. F. & Th.	14	14	0.07	0.42	19	12	0.07	0.41	12.5	5	0.04	0.18
Tarenna collinsae Craib	4	1	0.02	0.01	19	22	0.09	0.46	32.5	22.5	0.12	0.30
Randia wittii Craib	9	1	0.03	0.01	8	13	0.02	0.19	52.5	10	0.17	0.11
Legerstroemia duperreana Pierre	1	6	0.006	0.75	-	1	-	0.01	-	-	-	-
Cleidion spiciflorum Merr.	4	1	0.01	0.04	28	26	0.12	0.53	15	10	0.07	0.11
Diospyros dasyphlla Kurz	1	2	t	0.13	1	1	t	0.02	-	-		_
Melodorum fruiticosum Lour.	3	9	0.005	0.24	1	2	t	0.05	5	5	0.03	0.09
Dialium cochinchinense Pierre	3	5	0.009	0.22	3	1	0.01	0.54	2.5	-	0.01	-
Siphonodon celastrineus Griff.	8	8	0.04	0.18	4	3	0.01	0.20	2.5	-	0.005	-
Memecylon geddesianum Griff.	33	17	0.11	0.30	20	8	0.07	0.13	35	10	0.10	0.41
Acacia pennata Willd.	44	1	0.15	0.01	60	22	0.21	0.44	27.5	-	0.06	-
Eugenia cumini Druce	2	4	0.005	0.30	13	17	0.05	0.64	-	32.5	-	2.58
Nephelium hypoleucum Kurz	2	3	0.008	0.13	2	3	0.008	0.04	17.5	7.5	0.07	0.19
Phoebe sp.	2	14	0.02	0.48	5	7	0.02	0.13	5	12.5	0.01	0.57
Adenanthera pavonina Linn.	11	16	0.05	0.33	20	14	0.08	0.46	2.5	10	0.01	0.28
Unidentified 1	1	3	0.005	0.11	7	6	0.03	0.13	-	-	-	-
Schoutenia hypoleuca Pierre	1	1	t	0.08	73	9	0.27	0.10	2.5	-	0.01	-
Antidesma acidum Retz.	1	2	t	0.02	1	4	0.006	0.08	12.5	-	0.03	-
Eugenia aequea Burm. f.	1	1	t	0.03	12	7	0.04	0.25	10	-	0.04	-

Table 1. (Continued)

	Hopea ferrea type				Shore	a heni	<i>ryana</i> type		Ecotone			
	Densit		Basal	area	Densit	у	Basal a	rea	Dens	ity	Basal	area
Species	4.5 -< 10	≥10	4.5 -<1	0 ≱10	4.5 -< 10	≥ 10	4.5 -<10	≱ 10	4.5 -<1	0 >10	4.5 -<10	≱ 10
Garcinia speciosa Wall.	1	1	t	0.02	11	5	0.04	0.17	10	7.5	0.03	0.17
Garallia brachiata Merr.	5	1	0.01	0.07	-	3	-	0.59	5	5	0.02	0.07
Unidentified 2	-	1	-	0.009	•	3	-	0.09	-	-	-	-
Irvingia malayana Oliv. ex A. Benn.	-	3	-	1.17	-	7	-	2.31	-	-	-	-
Grewia paniculata Roxb.	_	2	-	0.06	-	1	-	0.16	-	2.5	-	0.09
Diospiros sp.	8	23	0.03	0.89	-	1	-	0.01	-	-	-	-
Paranephelium longifolium Lec.	-	1	-	0.03	2	4	0 01	0.15	-	5	-	0.08
Vitex sp.	-	2	-	0.04	1	2	t	0.03	-	5	-	0.26
Garcinia cowa Roxb.	-	1	-	0.07	1	1	t	0.06	-	-	-	-
Unidentified 3	5	18	0.02	0.50	-	-	-	-	-	-	-	-
Sindora siamensis Teijsm. ex Miq.	-	1	-	0.76	•	-	-	-	-	-	-	-
Lagerstroemia loudonii Teijsm. & Binn.	-	1	-	0.04	-	-	-	-	-	-	-	-
Ixora lobbii Loud.	1	ì	t	0.008		-	-	-	-	-	-	-
Casearia grewiaefolia Vent.	-	4	-	0.07	8	-	0.03	-	5	-	0.02	-
Cleistanthus gracilis Hook. f.	-	1	-	0.01	2	-	t	-	-	-	-	-
Helicia sp.	-	1	-	0.009	-	-	-	-	-	-	-	-
Miliusa mollis Pierre var. Sparsior Craib	2	1	0.006	0.01	-	-	-	-	-	-	-	-
Terminalia nigrovenulosa Pierre ex Laness.	-	1	-	0.06	2	2	0.008	0.08	-	2.5	-	0.04
Quercus sp.	-	1	-	0.07	-	-	-	-	-	•	-	-
Linociera microstigma Gagnep.	46	27	0.16	0.43	-	-	-	_	-	-	-	-
Anogeissus acuminata Wall.	-	2	-	0.04	•	- '	-	-	-	-	-	-
Pterocarpus macrocarpus Kurz	-	2	-	0.71	-	-	-	-	-	-	-	
Unidentified 4	10	7	0.03	0.10	-	-	-	-	-	5	-	0.28
Millettia leucantha Kurz	3	3	0.01	0.14	6	-	0.02	-	-	5	•	0.16
Quercus myrsinifolia Bl.	-	-	_	-	14	27	0.05	1.42	-	-	•	

Table 1. (Continued)

	1	Нореа	<i>ferrea</i> type		Shorea henryana type				Ecotone			
Species	Density		Basal area		Density		Basal area		Density		Basal area	
	4.5 -<10	<u>≱10</u>	4.5 -<10	≽ 10	4.5 -<10	≽10	4.5 -<10	≥10	4.5 -<10	≽ 10	4.5 -<1	0 ≥10
Baccaurea ramiflora Lour.	-	-	-	-	28	7	0.09	0.09	15	5	0.04	0.06
Pterospermum acerifolium Willd.	•	-	-	-	1	5	t	0.15	2.5	2.5	t	0.05
Knema globularia Warb.	-	-	-	-	55	24	0.22	0.40	5	-	0.01	-
Aphanamixis polystachya Parker	-	-	-	-	1	1	t	0.12	2.5	-	0.007	-
Donella lanceolata Aurb.	-	-	-	-	6	3	0.02	0.06	-	-	_	-
Cinnamomum iners Bl.	-	-	-	-	2	3	0.005	0.14	7.5	7.5	0.04	0.18
Glycosmis trifolia Spreng.	-	-	-	-	7	-	0.02	-	2.5	-	t	-
Hopea helferi Brand.	•	-	-	-	5	7	0.02	0.51	-	-	-	-
Parinari anamense Hance	-	-	-	-	4	4	0.01	0.06	-	-		
Croton oblongifolius Roxb.	•	-	-	-	15	3	0.07	0.03	2.5	-	0.006	-
Dipterocarpus turbinatus Gaertn. f.	-	-	-	-	2	7	t	2.32	2.5	-	0.02	-
Parkia sumatrana Miq.		-	-	-	2	6	0.009	0.2	-	10	-	3.90
Sandoricum koetjape Merr.	-	-	-	-	1	-	0.005	-	-	-	-	_
Dalbergia cochinchinensis Pierre	-	-	-	-	-	3	-	0.22	-	-	-	-
Artocarpus lakoocha Roxb.	-	-	_	-	1	-	t	-	-	-	-	-
Murraya paniculata Jack	_	-	-	-	6	3	0.02	0.04	-	-	-	
Mangifera pentandra Hook. f.	-	-	-	-	3	-	0.01	-	-	2.5	-	0.0
Bouea oppositifolia meissn. var. Microphylla Merr.	-	-	-		1	-	t	-	-	-	-	
Aquilaria crassna Pierre ex H. Lec.	-	-	-	-	4	2	0.01	0.02	-	-	_	-
Ficus annulata Bl.	-	-	-	-	-	1	-	1.58	-	-	-	-
Antiaria toxicaria Lesch.	-		-	-	1	2	t	0.07	-	-	-	-
Schima wallichii Korth	-	-	-	-	-	1	-	0.01	-	-	-	-
Pterocymbium javanicum R. Br.	-	-	-	-	1	-	t	_	-	-	-	-
Sterculia guttata Roxb.	-	-	-	-	-	1	-	0.05	-	_	-	-

Table 1. (Continued)

	<i>H</i>	opea j	<i>ferrea</i> type		Shorea henryana type				Ecotone			
Species	Density		Basal area		Density		Basal area		Density		Basal area	
	4.5 -<10	≽ 10	4.5-<10	≥ 10	4.5 -<10	≥10	4.5 -<10	≥ 10	4.5-<10	≥ 10	4.5 - < 10	≥10
Erythrina sp.	-	-	•	-	•	1	-	0.02		-		-
Bischofia javanica Bl.	-	-	-	-	-	1	-	0.03	-	-	-	-
Ixora ebarbata Craib.	1	-	t	-	2	-	0.005	-	7.5	-	0.02	-
Saprosma latifolium Craib	2	-	0.008	-	28	1	0.09	0.009	2.5	-	0.005	-
Tetrameles nudiflora R. Br.	1	-	t	-	2	3	0.009	0.15	-	-	-	-
Polyalthia virides Craib	1	-	0.008	-	2	1	0.007	0.01	-	-	-	-
Unidentified 5	1	-	t	-	4	6	0.02	0.14	-	-	-	•
Phoebe lanceolata	3	-	0.008	-	21	15	0.08	0.22	10	-	0.02	-
Lepisanthes tetraphylla Radlk.	2	-	0.007	-	43	4	0.14	0.06	7.5	-	0.02	-
Cananga latifolia Finet & Gagnep.	3	-	0.01	-	1	2	0.005	0.02	5	-	0.02	
Eugenia cinerea Kurz	1	-	t	-	2	1	0.005	0.07	12.5	-	0.04	-
Unidentified 6	1	-	t	-	-	1	-	0.01	7.5	-	0.04	
Protium serratum Engler	-	-	-	-	-	-	-	-	-	2.5	-	0.29
Celtis timorensis Span.	-	-	-	-	-	-	-	-	-	2.5	-	0.16
Xylia xylocarpa Taub.	-	-	-	-	-	-	-	-	-	2.5	-	0.02
Dalbergia cultrata Grah. ex Benth.	-	-	-	-	-	-	-	-	5	-	0.02	-
Peltophorum pterocarpum Back. ex Heyne	-	-	-	-	-	-	-	-	2.5	-	0.02	_
Unidentified 7	-	-	-	-	-	-	-	-	2.5	-	0.005	-
Total	592	562	2.19	30.01	768 .	.514	2.81	26.88	640	565	2.19	28.91

t: basal area less than 0.005 m²/ha

Table 2. Mean \pm standard deviation, and ranges (numbers within parentheses) for soil properties (0-15 cm depth) and topographic features of the three groups identified for the tropical semi-evergreen rain forest in Fig. 3 and 4.

Soil properties and topographic features	Hopea ferrea type	* Shorea henryana type	ecotone		
bulk density (gm/cc)	1.16* ± 0.06	1.04 ± 0.08	1.01 ± 0.04		
	(1.11 - 1.25)	(0.92 - 1.12)	(0.98 - 1.04)		
silt + clay (%)	56.40 ± 6.25	54.60 ± 11.12	64.50 ± 0.71		
	(48.5 - 63.5)	(38.5 - 64.0)	(64.0 - 65.0)		
pH	4.51 ± 0.78	3.69 ± 0.57	3.25 ± 0		
	(3.85 - 5.80)	(3.00 - 4.20)	(3.25)		
cation exchange capacity (m-equiv./100 gm)	7.02 ± 1.83	8.49 <u>+</u> 2.02	6.36 ± 0.65		
	(4.25 - 8.45)	(6.20 - 11.15)	(5.90 - 6.82)		
organic matter (%)	3.19 ± 0.90	3.71 ± 1.55	3.14 ± 0.31		
	(1.74 - 3.96)	(2.61 - 6.41)	(2.92 - 3.36)		
available phosphorus (ppm)	5.30 ± 1.04	4.70 ± 1.99	3.0 ± 0		
	(4.0 - 6.5)	(2.0 - 7.5)	(3.0)		
exchangeable cation (m-equiv./100 gm)					
potassium	0.23 ± 0.04	0.28 ± 0.07	0.38 ± 0.12		
	(0.17 - 0.27)	(0.23 - 0.40)	(0.29 - 0.46)		
calcium	0.57 ± 0.28	1.44 ± 0.90	0.66 ± 0.16		
	(0.30 - 1.00)	(0.62 - 2.84)	(0.55 - 0.77)		
magnesium	1.22 ± 0.45	1.72 ± 0.83	1.00 ± 00.41		
	(0.72 - 1.72)	(1.22 - 3.18)	(0.71 - 1.29)		
sodium	0.07 ± 0.02	0.07 ± 0.02	0.06 ± 0		
	(0.04 - 0.10)	(0.05 - 0.10)	(0.06)		
available moisture capacity (%)	11.85 ± 1.14	8.71 ± 1.87	6.76 ± 1.13		
	(10.31 - 13.26)	(7.58 - 11.89)	(5.96 - 7.56)		
elevation (m)	446* ± 20.74	534 ± 63.87	560 ± 0		
	(410 - 460)	(460 - 610)	(560)		
slope (degrees)	(0 - 6.8)	(4.5 - 15.8)	(0)		

^{*}These values are significantly different from Shorea henryana type values at the .05 level.

Hopea ferrea type and 75 in the Shorea henryana type. Eleven species of the Hopea ferrea type and 27 species of the Shorea henryana type were absent from the other. Only 54 species occurred in the ecotone and 5 of these were absent from the two types. Most of the 48 species present in both dominance-types were components of the lower tree stratum, small tree layer, and sapling and shrub layer. Important differences in basal area cover and density of the upper tree canopy did occur between the two dominance-types (Table 1). Hopea ferrea had a higher importance in the Hopea ferrea type while Shorea henryana, Quercus myrsinifolia and Dipterocarpus turbinatus had a higher importance in the Shorea henryana type.

The soil characteristics and topographic features of the two dominance-types and the ecotone are summarized in Table 2. Soils of the *Hopea ferrea* type exhibited the highest pH, available phosphorus and available moisture content while organic matter, exchangeable calcium and magnesium and cation exchange capacity were highest in the *Shorea henryana* type.

Relationships between environmental factors and sample stand distribution were determined by simple linear correlation of the environmental variables for a given sample against its score on the first and second axes of the ordination (Fig.3). Due to the small sample size, only five variables showed significant correlations with the sample distribution (Table 3). However, the percentage of variance accounted for in the first axis was low. The correlations accounted for 34, 34 and 60 percent of the available moisture capacity, bulk density and exchangeable calcium, respectively, in the first axis and for more than 49 percent of the organic matter and 64 percent of the available phosphorus in the second axis.

Stepwise multiple regression of environmental variables against the ordination values of the sample stands indicated significant correlations for both axes (Table 4). The correlations support the view that no single environmental factor can explain fully the distribution of the sample stands.

Size-class Distribution

The size-class structure of tropical semi-evergreen rain forest was similar for both the *Hopea ferrea* type and the *Shorea henryana* type. Size-class distributions were well described by the negative power curve ($R^2 = 0.96$ overall; $R^2 = 0.90$ for the *Hopea ferrea* type and $R^2 = 0.97$ for the *Shorea henryana* type) (Fig. 5), although the negative exponential curve also gave a good fit ($R^2 = 0.87$, 0.71, and 0.83, respectively). Only in the ecotone was its size-class distribution better described by a negative exponential ($R^2 = 0.95$) than a negative power curve ($R^2 = 0.92$).

Although the size-class distribution of the forest stand was characterized by a negative power function, the distributions of individual species were not. Five distinct

Table 3.	Correlation	coefficients	for	simple	linear	correlation	of	environmental
	variables wi	th ordination	ı val	ues.				

	Correlation coefficients (r)						
Variables	Axis 1	Axis 2					
bulk density	0.58*	0.24					
silt + clay	0.40	0.26					
pH	0.51	-0.40					
cation exchange capacity	-0.34	-0.50					
organic matter	-0.29	-0.70*					
phosphorus	0.07	-0.80**					
potassium	-0.29	0.25					
calcium	-0.77**	-0.14					
magnesium	-0.37	-0.03					
sodium	0.09	-0.38					
available moisture capacity	0.58*	-0.50					
elevation	-0.42	0.06					
slope	-0.55	-0.02					

- * Significant at the .05 level
- ** Significant at the .01 level.

Table 4. Stepwise multiple regression equations for environmental variables against ordination values.

The dependent variable is: X

$$X = -5.1137 - 23.9920$$
 calcium + 54.8566 bulk density + 8.5320 pH - 0.7512 slope - 2.3132 cation exchange capacity \pm 5.5556 ($R^2 = 0.97$, P < 0.001)

The dependent variable is: Y

Y =
$$120.8290 - 3.8100$$
 phosphorus -0.2895 (silt + clay) -5.8804 calcium -7.0631 organic matter -6.7176 pH ± 3.2809 ($R^2 = 0.96$, P< 0.001)

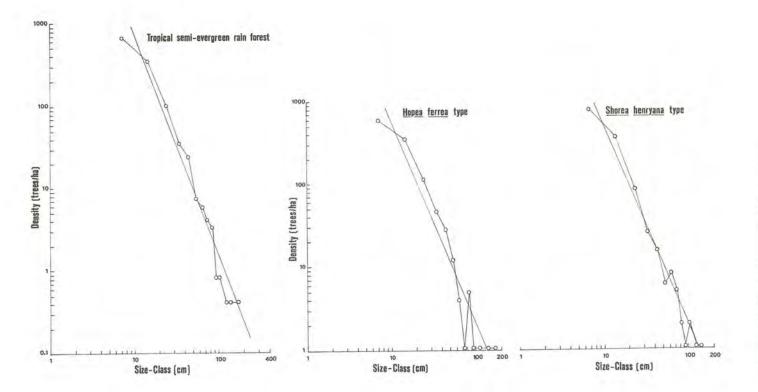


Figure 5. Size-class distributions for all stems from the tropical semi-evergreen rain forest, the *Hopea ferrea* type, and the *Shorea henryana* type. Size-classes are in 10 cm dbh intervals, except that the first interval is truncated by the lower limit of sampling (4.5-9.9 cm dbh). Lines were fitted to the data by the negative power curve and are described by $y = 374,524.02 \text{ x}^{-2.70}$ for the tropical semi-evergreen rain forest, $y = 159,654.79 \text{ x}^{-2.44}$ for the *Hopea ferrea* type and $y = 170,165.20 \text{ x}^{-2.47}$ for the *Shorea henryana* type.

patterns of size-class distribution occurred. In both dominance-types most species of the lower tree stratum and the small tree layer approximated the negative exponential (eg. Hydnocarpus ilicifolius, Walsura trichostemon, Memecylon ovatum) and negative power function (Hopea ferrea, Hydnocarpus castaneus, Eugenia cumini) (Fig. 6). Some species fitted both functions such as Aglaia pirifera, which was well fitted by the negative exponential in the Shorea henryana type but better described by the negative power function in the Hopea ferrea type.

Among upper canopy species, three other patterns were evident. First, some species were characterized by a steeply declining curve in the small size-classes followed by a plateau. Shorea henryana in the Shorea henryana type exhibited this pattern (Fig. 6). Secondly, Irvingia malayana and Parkia sumatrana had a uniform distribution with equal occurrence of individuals in all size-classes. Thirdly, some species, such as Lagerstroemia duperreana, had more large stems (Fig. 6).

Species-environment Relationships

Correlations between environmental variables and the importance values of individual species were estimated by using stepwise multiple regression. Of the 18 species used for prediction, 13 yielded statistical significance. However, no single environmental factor seemed to explain the distribution of the species (Table 5). The models follow the general equation

 $Y = a + b_1 x_1 + b_2 x_2 + ...b_n x_n + SE,$

where Y = dependent variable,

a = Y intercept,

b = partial regression coefficient,

x = independent variable,

SE = standard error of estimate.

The leading dominant species of the upper canopy, *Hopea ferrea*, exhibited distributions which seemed to be related to soil fertility. It showed a negative correlation with potassium and soil pH and a positive relationship to percent silt + clay and organic matter. Greatest importance occurred on sites where soil pH ranged from 3.85 - 4.15. Lower importance occurred at a higher soil pH (5.8) where the stands were located on the edge of the semi-evergreen rain forest and where surface fire might have spread from the adjacent dry deciduous dipterocarp forest. The other leading dominant species, *Shorea henryana*, showed relationships with both topography and

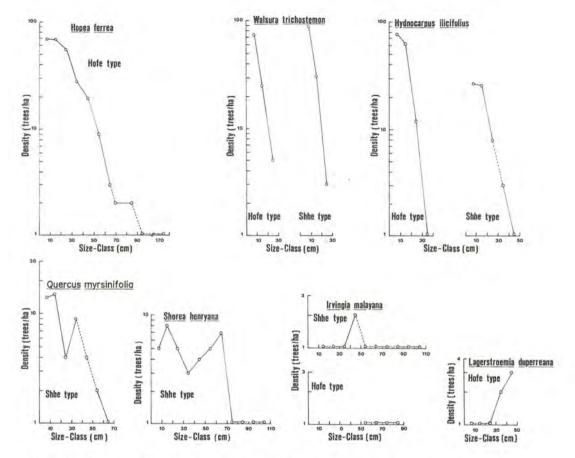


Figure 6. Size-class distributions of selected species in the Hopea ferrea type (Hofe type) and the Shorea henryana type (Shhe type). Size-classes are as in Fig. 5. Dashed lines indicate empty sizeclasses.

Table 5. Stepwise multiple regression equations for environmental variables against importance value of the individual species.

Hopea ferrea Pierre	Ŷ	=	322.1641 - 632.2478 potassium - 32.1884 pH + 0.8422 (silt + clay) + 9.8265 organic matter ± 4.6838
Shorea henryana Pierre	Ŷ	=	$(R^2 = 0.99, P < 0.05)$ -110.3050 + 0.2395 elevation + 1.2745 slope + 3.9956 cation exchange capacity - 330.4995 sodium \pm 6.2575 $(R^2 = 0.94, P < 0.01)$
Hydnocarpus ilicifolius King	Ŷ	=	$16.2855 - 6.9973$ calcium $- 611.6247$ sodium $- 7.5475$ cation exchange capacity $+ 4.3910$ organic matter $+ 0.1333$ elevation $+ 3.7106$ available moisture capacity ± 3.4472 ($\mathbb{R}^2 = 0.97$, $\mathbb{P} < 0.01$)
Walsura trichostemon Miq.	Ŷ	=	9.9014 + 2.9860 calcium - 0.2075 (silt + clay) + 39.0088 potassium + 3.4049 organic matter - 1.2250 cation exchange capacity \pm 1.8934 ($R^2 = 0.93$, $P < 0.01$)
Aglaia pirifera Hance	Ŷ	=	- 130.9021 - 1.2390 available moisture capacity + 126.6302 potassium - 5.4632 magnesium + 75.8225 bulk density + 0.1017 elevation \pm 6.6706 ($\mathbb{R}^2 = 0.88$, $\mathbb{P} < 0.05$)
Eugenia cumini Druce	Ŷ	=	- $55.8327 + 0.1447$ elevation - 0.8405 slope + 4.5633 magnesium - 2.7072 cation exchange capacity + $1,1400$ available moisture capacity ± 1.4225 ($R^2 = 0.98$, $P < 0.01$)
Parkia sumatrana Miq.	Ŷ	=	,

Table 5 (Continued)

Hydnocarpus castaneus Hook.f. & Th.	Ŷ	=	$3.3636 + 5.0507$ magnesium $- 2.2408$ calcium $- 9.2030$ potassium ± 2.1578 (R ² = 0.67, P < 0.05)
Metadenia trichotoma Bakh.f.	Ŷ	=	- 83.6089 + 0.1376 elevation + 7.7779 calcium + 2.3606 available moisture capacity - 1.7275 phosphorus \pm 1.1286 ($\mathbb{R}^2 = 0.99, P < 0.05$)
Linociera microstigma Gagnep.	Ŷ	=	- 19.3043 - 10.9339 organic matter + 0.1458 elevation \pm 0.1938 ($R^2 = 0.99, P < 0.001$)
Memecylon geddesianum Craib	Ŷ	=	-71.8219 + 9.7531 pH + 0.0856 elevation $-3.0544 \text{ organic matter}$ $+0.1098 \text{ (silt } + \text{clay)} \pm 1.8978$ $\text{(R}^2 = 0.95, P < 0.01)$
Dipterocarpus turbinatus Gaertn. f.	Ŷ	=	$55.7196 - 0.7741 \text{ (silt + clay)} \pm 0.6409$ (R ² = 0.99, P < 0.01)
Melodorum fruticosum Lour.	Ŷ	=	- $8.2221 + 4.7915 \text{ pH} - 1.1407$ phosphorus - $1.9949 \text{ calcium } \pm 0.6005$ ($R^2 = 0.99, P < 0.01$)

fertility. Elevation, slope and cation exchange capacity showed a positive relation with *Shorea henryana*. Its distribution indicated that the greatest importance occurred on sites at mid elevation (540-610 m) with a slight slope ($< 13^{\circ}$) and cation exchange capacity ranging from 8-11 m-equiv./100 g of soil.

DISCUSSION

Vegetation Structure

The classification of sample stands into two dominance-types following the dendrogram, namely the *Hopea ferrea* type and the *Shorea henryana* type, were also confirmed by ordination. Two stands from the ecotone grouped themselves together with the dominance-type due to the species composition being somewhat similar to those of the two main types. It should be noted that the *Shorea henryana* type at

Sakaerat has never been mentioned in previous studies (SABHASRI *et al.*, 1968; SMITINAND *et al.*, 1968; WACHARAKITTI, INTRACHANDRA & MUNGKORNDIN, 1980; VISARATANA, 1983).

Nearly identical basal areas resulted from fewer large trees but a greater number of small trees in the *Shorea henryana* type than in the *Hopea ferrea* type. Basal areas from this study were similar to those of the tropical semi-evergreen rain forest in the Nam Pong basin $(25 \text{ m}^2/\text{ha}, \ge 10 \text{ cm dbh}; \text{Bunyavejchewin}, 1979)$ and in the Nam Prom basin $(35 \text{ m}^2/\text{ha}, \ge 4.5 \text{ cm dbh}; \text{Tsutsumi et al.}, 1983)$. VISARATANA (1983) found a basal area of $31 \text{ m}^2/\text{ha}$ ($\ge 4.5 \text{ cm dbh}$) in the *Hopea ferrea* type at Sakaerat. WACHARAKITTI, INTRACHANDRA & MUNGKORNDIN (1980), however, estimated basal areas of the *Hopea ferrea* type at Sakaerat at $65 \text{ m}^2/\text{ha}$, ($\ge 10 \text{ cm dbh}$) which seems high when compared with the other figures.

Floristically, the two types are similar; 5/6 of the species in the Hopea ferrea type and 2/3 of those in the Shorea henryana type (48 species) were found in other type. The species of the upper canopy and some species in small the tree layer of the Shorea henryana type, such as Quercus myrsinifolia, Parkia sumatrana, Dipterocarpus turbinatus, Hopea helferi and Knema globularia, were absent from the Hopea ferrea type. The primary difference was the complete absence of Hopea ferrea in the Shorea henryana type. The 92 tree and shrub species recorded in this study are almost 50 percent more than recorded in previous studies (SABHASRI et al., 1968; SMITINAND et al., 1968; VISARATANA, 1983), mainly because of the high species richness of the Shorea henryana type.

Generally, in temperate forests, the size-class structure of old-age stands with little or no disturbance is best described by the negative exponential curve or J-shaped distribution, which implies constant rates of mortality from one size-class to the next (LEAK, 1965; MULLER, 1982). Individual species are best described by the negative power curve which assumes declining mortality with size (ROBERTSON, WEAVER & CAVANAUGH, 1978). However, few size-class analyses have been done for tropical forests. In this study, size-class distributions of the semi-evergreen rain forest in general and of the two types in particular were well fitted by the negative power curve. Individual species of the lower tree stratum and the small tree layer were fitted by both the negative exponential distribution and negative power curve. The dominant species of the upper canopy, Hopea ferrea, was best described by a negative power function while Ouercus myrsinifolia, Irvingia malayana, Dipterocarpus turbinatus and Lagerstroemia duperreana were fitted poorly by both curves. Using either distribution as a basis of comparison, the lower tree stratum and small tree layer species exhibited more negative slopes than the species of the upper tree stratum, implying greater mortality than in the dominant species of the upper canopy. This seems resonable because the canopies of the small tree layer and lower stratum are close together, and species there might be expected to have higher mortality than the upper canopy species.

Shorea henryana and Quercus myrsinifolia exhibited discontinuous distributions with secondary peaks of density in the larger classes following the decline of the smaller size-classes. This may reflect some slight local disturbance which interrupted their regeneration, or natural fluctuations in climate which affect reproduction or survival. Irvingia malayana exhibited no descending curve because its seeds are dormant for several months before germination and are usually eaten by animals. This species probably does not find conditions optimal in this community and may disappear. Lagerstroemia duperreana, a light-demanding species, had more big stems than smaller because it cannot regenerate in shade.

Community and Species Distributions

The ordination of sample stands, soil properties and topographic features for the twelve stands in the tropical semi-evergreen rain forest revealed strong correlations which support the view that the distributions of dominance-types in this region are determined by complex interactions of environmental variables. Average soil properties and topographic features differed between the dominance-types. Although the *Shorea henryana* type grows on more fertile soil than the *Hopea ferrea* type, its basal area cover is lower because of lower soil pH and moisture. The availability of nitrogen is inhibited by a low soil pH. Soil pH also serves as an indicator of the two major nutrients calcium and magnesium. Calcium plays an important role in the absorption of and selectivity for cations (BLACK, 1968) and is also an indicator of forest soil fertility (WARING & MAJOR, 1964). Thus, low availability of calcium in acid soils may decrease availability of the other nutrients to plants. The *Shorea henryana* type, which occupies the slope areas, may promote the occurrence of windthrow which could reduce the overall basal area cover.

The relationship between soil characteristics and vegetation has been determined in several locations in previous studies. Newbery & Proctor (1984) found no association between soil and vegetation in dipterocarp forest and forest over limestone in Gunung Mulu National Park, Sarawak. Some studies have also indicated that vegetation in the tropical rain forest is more closely related to topography than to soil factors (Austin & Greig-Smith, 1968; Wong & Whitmore, 1970; Ashton, 1976). Several studies have found soil fertility to be an important factor influencing species distributions, however (Ashton, 1964; Marchand, 1973; Kutintara, 1975; Sukwong & Kaitpraneet, 1975; Goldberg, 1982; Bunyavejchewin, 1983, 1985; Newbery & Proctor, 1984). This study suggests that topography (elevation) and soil fertility (eg. potassium, calcium, organic matter) may play an important role in determining the distributions of species in the tropical semi-evergreen rain forest. Many studies have also found that potassium and calcium influence species and community distributions (Wikum & Wali, 1974; Kutintara, 1975; Bunyavejchewin, 1983, 1985).

ASHTON (1960, 1963; cited in ROBBINS & WYATT-SMITH, 1964) have found that soil moisture is an important factor controlling species components in the dipterocarp forest in Borneo. In this study, higher moisture content was found in the flat area dominated by *Hopea ferrea* than in the sample plots dominated by *Shorea henryana* and other associated species, such as *Parkia sumatrana*, *Quercus myrsinifolia* and *Tarenna collinsae*. The indirect gradient analysis of the first axis of the ordination (Table 3) also confirms this relationship. The interactions of moisture content, soil pH, and soil nutrients may play a major role in influencing species growth on those sites.

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